

## ABERRANT MEIOTIC BEHAVIOUR IN SOME MEMBERS OF FAMILY SOLANACEAE FROM NORTH INDIA

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### ABSTRACT

The present paper shows the affect of abnormal meiosis on pollen fertility. Out of 12 investigated wild species of the family Solanaceae, 9 species viz. *Cestrum elegans*, *C. nocturnum*, *Datura stramonium*, *Nicotiana tabacum*, *Physalis angulata*, *P. peruviana*, *Solanum pseudocapsicum* and *S. verbascifolium* show abnormal meiotic course. These abnormalities are in the form of multivalent, secondary association of bivalents, stickiness, early separation of bivalents, unoriented bivalents at diakinesis/ M-I, laggards, bridges during both anaphase and telophase stages, abnormal microsporogenesis and pollen sterility. Cytomixis is also observed in some species. Reduction in pollen fertility varies among different species which mainly depends upon the quality and quantity of meiotic abnormalities. Much reduced pollen fertility (38.73 %) due highly abnormal meiosis is noticed in *Cestrum elegans*.

**KEYWORDS:** Male Meiosis, Meiotic Abnormalities, Pollen Sterility, Solanaceae, Kangra

### INTRODUCTION

Meiosis is a cytological basis for gametogenesis and inheritance in eukaryotic organisms and maintains genomic stability as well as integrity over sexual life cycles. Meiosis involves specialized cell division which is a dynamic cellular process controlled by the action and synchrony of many genes (Baker *et al.*, 1976; Schwarzacher, 2003), and action and function of these genes is also influenced by environmental factors such as high and low temperatures, chemicals, radiations and nutrition. Different genes have been identified in plants which condition the different events in meiosis. Basic steps of meiosis involve molecular and cellular events, such as DNA and chromosome replication, chromosome pairing, synapsis and recombination, chromosome segregation and cytokinesis (Cai and Xu, 2007). Balanced chromosome segregation followed by normal cell division and formation of a bipolar microtubule based spindle is required for normal meiosis. Conversely any discrepancy at molecular or cellular level during meiosis may perhaps causes male sterility (Glover *et al.*, 1998). Meiotic abnormalities which generally affect the pollen viability have troubled sexual reproduction. The wild species produce copious and highly viable pollens than that of cultivated one (Stout and Clark, 1924). The present study is determined on wild species of family Solanaceae.

The family Solanaceae Juss. comprises of 100 genera and 2,500 species (Olmstead and Bohs, 2007). Members of the family are found in all temperate and tropical continents with maximum biodiversity in Western hemisphere (Olmstead *et al.*, 2008). In India, 26 genera and 131 species mostly found in Himalaya and mountains of South India with many as cultivated one (Kumar and Subramaniam, 1986). The family has a great importance as source of food, medicine, narcotics and floristics. Some species are used as ornamentals (e.g., *Cestrum diurnum*, *C. nocturnum* and *C. elegans*) or as medicinal plants (e.g., *Atropa belladonna*, *Withania somnifera*, *Datura* spp. and *Solanum* spp.) or many are toxic because

of the presence of alkaloids. In India, *D. stramonium* is a common plant in foothills of dry slopes in Western Himalayas up to 1800 m altitude. In India, it grows as a wasteland weed and is cultivated for its alkaloids in India and Europe.

The present paper is a part of the present study on chromosome counts of Gamopetalous members from District Kangra (H.P.), North India. This paper mainly concentrating on detailed meiotic abnormalities presently encountered in 12 wild species of family Solanaceae.

## MATERIALS AND METHODS

Plant materials of wild taxa of Solanaceae family were collected throughout the year in 2008-2010 from different localities of Kangra, Himachal Pradesh of North India (Table 1). Voucher specimens are deposited in Herbarium, Department of Botany, Punjabi University, Patiala (PUN). Appropriate sized flower buds were fixed in Carnoy's fixative (6:3:1= absolute alcohol: chloroform: glacial acetic acid v/v/v) for 24 hrs and preserved in 70% alcohol at 4°C. For meiotic studies the appropriate sized anthers were squashed in 1% acetocarmine. Apparent pollen fertility was estimated by mounting mature pollen grains in glycerol-acetocarmine (1:1). Normal well filled and deeply stained pollens were taken as fertile while shrivelled up and unstained pollens as sterile. Pollen size was measured using ocular micrometer. Photomicrographs of meiotic cells are made from freshly prepared slides using Nikon digital imaging system.

**Table 1: Information on Taxa, Voucher Data, Accession Number, Chromosome Number, Ploidy Level and Meiotic Abnormalities in Presently Investigated Species of the Solanaceae Family from District Kangra, Himachal Pradesh**

Name of Taxa	Locality	Altitude (m)	Accession Number (PUN)	Chromosome number (2n)	Ploidy level	Meiotic Abnormalities	Pollen fertility (%)	Pollen size (µm)
<i>Cestrum elegans</i> (Brongn. ex Neumann) Schtdl.	Dharamshala	1500	56037	16	2x	Stickiness, unoriented bivalents, laggards, bridges, micronuclei	38.73	18.75 - 31.87
<i>C. nocturnum</i> L.	Dharamshala	1500	56451	16	2x	Stickiness, laggards	83.58	-
<i>Datura stramonium</i> L.	Dehra Nurpur	490 710	53200 57891	24 24	2x 2x	Stickiness, multivalent, cytotoxicity	81 84	26.25 - 28.12 26.25 - 28.12
<i>Nicotiana tabacum</i> L.	Chhota Banghal; Dyot Boh	765 1670	53201 56416	48 48	4x 4x	Secondary association of bivalents, stickiness, unoriented bivalents, laggards, micronuclei	89 91	19.87 - 19.87 19.50 - 22.50
<i>Physalis angulata</i> L.	Nagrota Surian Masroor	530 620	53202 53203	48 48	4x 4x	Unoriented bivalents, secondary association of bivalents	94 93	26.25 - 26.25 26.25 - 26.25
<i>Physalis peruviana</i> L.	Palampur; Bandla	1221	52460	48	4x	Secondary association of bivalents, unoriented bivalents, multivalent, laggards, bridges, cytotoxicity, abnormal microsporogenesis	76	27.00 - 30.00
<i>Solanum indicum</i> L.	Dharamshala	1500	53192	24	2x	-	100	-

Table 1-Cond.,

<i>Solanum nigrum</i> L.	Mcleodganj	1780	53029	48	4x	-	100	16.87 - 18.75
	Nagrota Surian	530	53033	24	2x		98	15.00 - 22.62
	Bankhandi	557	53185	48	4x		99	15.00 - 22.50
	Galua	595	53186	24	2x		87	15.00 - 30.00
	Bassa	490	53187	24	2x		99	22.62 - 30.00
	Dharamshala	1500	53188	24	2x		100	18.00 - 18.00
	Palampur; Bandla	1221	53189	48	4x		98	26.25 - 26.25
	Chhota Banghal;	2037	53190	48	4x		96	18.75 - 22.75
	Dyot	2250	53191	48	4x		98	18.75 - 18.75
<i>Solanum pseudocapsicum</i> L.	Bujling					Early separation of bivalents		
	Near Dharamshala	1450	56440	24	2x		97	15.00 - 19.50
<i>Solanum surattense</i> Burm.f.	32 Meel	620	53193	24	2x	-	99	16.87 - 17.62
	Pargor	780	53194	24	2x		98	16.87 - 16.87
<i>Solanum verbascifolium</i> L.	Dehra	490	53199	24	2x	Chromatin stickiness	100	15.00 - 15.00
<i>Solanum viarum</i> Dunal	Nagrota Surian	530	53195	24	2x	-	76	20.62 - 28.12
	Dharamshala	1500	53196	24	2x		80	20.62 - 21.75
	Palampur; Bandla	1221	53197	24	2x		83	21.75 - 21.75
	Chhota Banghal;	2200	53198	24	2x		87	21.75 - 21.75
	Loharadi							

## RESULTS AND DISCUSSIONS

Information on taxa, voucher data, chromosome number, ploidy level, meiotic abnormalities, pollen fertility and pollen size in presently investigated 12 species of 5 genera covering 27 wild populations of the Solanaceae family from district Kangra (Himachal Pradesh), North India is compiled in Table 1. Details of abnormal taxa are further discussed.

### • *Cestrum Elegans* (Brongn.) Schltdl

Diploid species with  $2n = 16$  depicts highly abnormal meiosis with lot of spindle affected abnormalities. Complete chromatin stickiness at diakinesis and metaphase-I is observed in most of the cells. It is quite difficult to distinguish the bivalents. The non-congregation of bivalents at the equatorial plate (Figure 1) and occurrence of unoriented bivalents (1-2 per PMC) at metaphase-I (Figure 2) are quite common though few PMCs show the presence of distinct 8 bivalents (Figure 3). During anaphase-I, the chromosomes do not segregate in a regular fashion. In most of the cells, the segregated chromosomes failed to converge at the poles and further grouped into variable sized nuclei at telophase-I. Similar pattern is observed during Meiosis II. Telophase-II products are highly affected with formation of several (2-6) micronuclei (figure 4). Sometimes these constitute their own cytoplasm or it may be included within macronuclei of tetrasporads. A large number of PMCs are observed with (1-2) bridges also (Figure 5). Microsporogenesis is also abnormal as 1-7 micronuclei observed which affect about 93.77% tetrads (Figure 6). As a result of all these abnormalities a total of 92.23% meiotic product is affected (Table 2). Further pollen grains show heterogeneous size that varies from 3.75-16.95 $\mu$ m in sterile pollen grains to 15.37-31.87 $\mu$ m in fertile pollens (Figure 7). Mostly small sized pollen grains are sterile. Anomalous meiotic behaviour as a whole leads to 61.27% pollen sterility.

**Table 2: Number of Cells Analyzed during Meiosis and Percentage of Abnormal Cells Observed in Each Meiotic Phase in *Cestrum Elegans***

Meiotic Phase	Total PMCs Observed	Abnormal PMCs Number (%age)	Abnormalities
Diakinesis	42	42 (100)	Stickiness
Metaphase I	184	39 (21.19 ) 49 (26.63 ) 96 (52.17 )	Stickiness Unoriented bivalents Not congregate at equatorial plate
Anaphase I	139	94 (67.62) 32 (23.02)	Laggards Bridges
Telophase I	199	150 (75.37) 26 (13.06)	Micronuclei Bridges
Prophase II	108	87 (80.55)	Micronuclei
Metaphase II	77	69 (89.61)	Unoriented chromatids
Anaphase II	129	111 (86.04) 18 (13.95)	Laggards Bridges
Telophase II	185	142 (76.75) 21 (11.35)	Micronuclei Bridges
Tetrad	289	271 (93.77)	Micronuclei
Pollen grains	798	489 (61.27)	Sterile pollens

- ***Cestrum Nocturnum* L.**

In some of the PMCs (6.33%) of the diploid cytotype ( $2n = 16$ ) (Figure 8), the bivalents show stickiness resulting into 3-5 groups at metaphase-I (Figure 9). Most of the cells have normal segregation at anaphase-I, with few (9.45%) having 1-2 laggards at telophase-I (Figure 10). This stickiness further moves to meiosis-II. A few cells (7.89%) observed with laggards at anaphase-II. Pollen fertility is 83.58% and pollen size ranges from 22.50-30.00 $\mu$ m.

- ***Datura Stramonium* L**

In India, *D. stramonium* is a common plant in foothills of dry slopes at 1800m in Western Himalayas. It grows as a wasteland weed and is cultivated for its alkaloids in India and in Europe. Meiotic observations on the two populations, differing in flower color (pink and white) of species from different localities, depict  $2n = 24$  (Figure 11). Meiotic course in both the populations is abnormal as an association of bivalents is found to be quite common (Figure 12). These associations are sometimes in the form of interbivalent connections (4-8) or secondary associations or 1-2 multivalents. During metaphase-II, 1-2 unoriented chromosomes are observed (Figure 13). Cytomixis at diakinesis and metaphase-I is noticed which results into PMCs with lower and higher chromosome numbers (Figures 14, 15). In spite of all these irregularities, microsporogenesis is balanced leading to high (81-84%) pollen fertility.

- ***Nicotiana Tabacum* L**

Meiotic observations made on two populations of the species, differing in flower color: white in Chhota Banghal population and pink in Boh population, show  $2n = 48$  (Figure 16). Meiosis is quite abnormal in both the populations (Table 3). At diakinesis/ metaphase-I, multivalent or associations of bivalents (Figure 17), chromatin stickiness and 1-2 non-synchronized bivalents (Figure 18) are observed. During anaphases and telophases, 1-6 laggards are noticed (Figures 19, 20). Microsporogenesis is abnormal with the formation of monads, dyads, triads and tetrads with 1-2 micronuclei, besides normal tetrads. In spite of these meiotic irregularities, pollen fertility is high (89-91%) in both the populations and pollen size varies 19.87-22.50 $\mu$ m.

**Table 3: Meiotic Abnormalities at Different Meiotic Phases in Two Accessions of *Nicotiana Tabacum***

Accessions	Meiotic Phase/s	Total PMCs Observed	Abnormal PMCs Number (%age)	Abnormalities
<b>Accession-1</b>	Diakinesis/ Metaphase I	64	16 (25) 6 (9.37 )	Chromatin stickiness Non-synchronized bivalents
	Anaphase I/ Telophase I	74	8 (10.81)	Laggards
	Anaphase II/ Telophase II	115	15 (13.04)	Laggards
	Microsporogenesis	159	15 (9.43)	Tetrad with micronuclei
<b>Accession-2</b>	Diakinesis/ Metaphase I	94	21 (22.34) 29 (30.85 ) 8 (8.51)	Multivalent formation Chromatin stickiness Non-synchronized bivalents
	Anaphase I/ Telophase I	82	21 (25.60)	Laggards
	Anaphase II/ Telophase II	177	42 (23.72)	Laggards
	Microsporogenesis	107	8 (7.47) 5 (4.67) 4 (3.73) 2 (1.86)	Monad Triad Triad with micronucleus Tetrad with micronucleus

- ***Physalis Angulata* L**

Two tetraploid populations with  $2n = 48$  are worked out. Meiosis in population-1 is normal but abnormal in population-2. Un-oriented bivalents (1-2 per PMC) in 27.27% PMCs and chromatin stickiness in the form of complete clumps/ association in groups are observed in 72.72% PMCs (Figures. 21, 22). Microsporogenesis is normal in both the populations leading to high pollen fertility (93-94%).

- ***Physalis Peruviana* L**

The tetraploid cytotype with  $2n = 48$  show highly abnormal meiosis. The bivalents have the tendency of sticking together either in the form of secondary associations or sometimes in the form of clear multivalents (Figures. 23, 24). In some of the PMCs, the existence of varied number of quadrivalents (1-5) is quite clear though the most common configuration is that of  $1_{IV} + 22_{II}$  (Table 4). However, the stickiness due to secondary associations is more prominent with different groups of bivalents. Among these the most common association is group of three (29.03%), followed by six (16.13%), seven (14.30%), five (12.90%), four (9.68%), nine (6.45%), two (5%) and ten (3.22%). Most of the bivalents are properly oriented at the equatorial plate but few (1-3) show un-orientation during metaphase-I in 17.96% PMCs (Figure 25). Further laggards are observed at anaphase-I/telophase-I (13.34%), and anaphase-II/ telophase-II (6.96%) (Figure 26). Besides this, chromatin bridges (1-2) are observed in 8.13% PMCs. Cytomictic channels and actual transfer of chromatin material is observed from early prophase to late telophase-II. Though, the maximum frequency of such cells is at prophase-I. In many cases 3-4 PMCs are involved in chromatin transfer. The chromatin transfer is either partial or complete. As a result, some PMCs are observed with double the chromosome number (4.73% PMCs) or totally empty (1.73% PMCs) or with extra chromatin material (8.66%). Due to the presence of various meiotic abnormalities, the microsporogenesis is highly abnormal. Besides 82.05% normal tetrads, monads (3.94%), triads (4.67%) and tetrads with micronuclei (9.34%) are also observed (Figure 27). Due to cytomixis some of the monads are without any chromatin material, whereas in some others cytomictic channels are quite evident. These meiotic abnormalities lead to decrease in pollen fertility (76%).

**Table 4: Chromosomal Associations at Metaphase-I in *Physalis Peruviana***

PMCs Observed		Configurations		
Number	%age	IV	II	I
10	37.00	1	22	0
6	22.22	1	21	2
4	14.81	2	20	0
4	14.81	3	17	2
3	11.11	5	14	0
Total: 27	99.95	12	94	4
Average frequency/PMC		00.44	03.48	00.14
%age of chromosomes involved		03.66	14.50	00.29

- ***Solanum Pseudocapsicum* L**

Meiosis in diploid population ( $2n = 24$ ) is almost normal but 14.78% cells are observed with early separation of 2-6 bivalents at metaphase-I (Figure 28). Pollen fertility is 100%.

- ***Solanum Verbascifolium* L**

Diploid population ( $2n = 24$ ) of species show chromatin stickiness with the occurrence of 1-2 unoriented bivalents in 29% PMCs (Figure 29). Pollen fertility is 100%.

The presence of multivalents in diploids (eg *Datura stramonium*) indicates the occurrence of heterozygote translocations between two/ three pairs of chromosomes. The plants with such type of meiotic configurations are termed as structural heterozygotes or structural hybrids. Such type of structural changes in chromosomes may increase the amount of genetic variability in the gametes by forming new genetic linkage groups which may be used for adaptation to adverse environmental conditions (Talukdar, 2009). The presence of few multivalent associations is an evidence for segmental allopolyploidy, where the parental genomes are partially homologous as a case earlier seen in *Brachiaria* (Mendes-Bonato, 2000). In autopolyploids, pairing is characterized by multiple forms of chromosome associations. Polyploids can also display secondary modifications (Stebbins, 1971). Reduction in fertility in polyploids has been identified mainly due to meiotic abnormalities, genetic causes that are independent of meiotic aberrations and incidental phenotypic effects of polyploidy as presently observed in *Physalis peruviana*.

Intense clustering or clumping during any phase of cell cycle involving few chromosomes to entire chromosome complement is presently seen in 4 species. In these species, stickiness is more common at metaphase-I than at metaphase-II. In severe cases, the chromosomes are unfeasible to separate and lead to the formation of single or varying number of pycnotic micronuclei in microspores as the case observed in tetraploid *Brachiaria brizantha* (Mendes-Bonato *et al.*, 2001). Chromatin stickiness may be caused by genetic or environmental factors (Consolaro and Pagliarini, 1996). Gaulden (1987) hypothesized that stickiness may be caused by functioning of one or two types of non-histone proteins involved for chromatin separation and further segregation. However, the degree of chromatin stickiness depends upon the number of the target protein molecules affected by its inhibitors, which shows that not all the cells are affected by this phenomenon.

Secondary associations are the loose associations of bivalents without any chiasmata formation and are differentiated from multivalents where chiasmata formation occurs among two or more non-homologous chromosomes. It is suggested that chromosomes with secondary associations could be complete homologous or partially and reflect

polyploid origin of the species as the case seen in *Nicotiana* and *Physalis* spp. Such type of associations seems to indicate basic chromosome number for the taxon. These associations are used to presume basic chromosome number in many genera and species (Darlington and Moffet, 1930; Mukherjee and Datta, 2006). In present study, the phenomenon is observed in both *Cestrum* spp. It is based on the idea that homologous bivalents have tendency to attract each other (Heilborn, 1936) due to more distantly related chromosomes and reported in number of plants: *Ocimum* spp. (Mukherjee and Datta, 2006), *Physalis peruviana* (Bala and Gupta, 2011), *Senecio* and *Gynura* spp. (Gupta *et al.*, 2010). The formation of five groups in *Senecio laetus* (Gupta *et al.*, 2010) due to secondary associations of bivalents clearly indicates the  $x = 5$  as the original base number which supports the idea of many workers.

The phenomenon of transfer of chromatin material from one PMC to another was named for the first time as 'cytomixis' by Gates in 1911. Different workers gave different opinions as possible cause of the cytomixis such as due to effect of fixation (Haroun, 1995); pathological factors (Brown and Bertke, 1974; Omara, 1976); physiological changes (Bahl and Tyagi, 1978), temperature (Narain, 1976) and genetic influence (De and Sharma, 1983; Kaul and Nirmala, 1991). This abnormality is noticed in presently investigated populations of *Datura stramonium* and *Physalis peruviana*.

Bivalents that are not lying on the equatorial plate are known as un-oriented or non-synchronized bivalents. The final orientation of chromosomes at metaphase-I normally will determine the disjunction pattern of chromosomes during anaphase-I. Univalents usually lag behind and left out of the nuclei at telophase-I. The sister chromatids may separate at anaphase-I, but frequently causes lagging and may also be left out of daughter nuclei but sometimes they may be included in the normal nuclei. Ultimately they do not become a part of normal nucleus and form very small non-functional pollen grains. Multivalents in polyploids may behave variously according to their metaphase orientation and subsequent segregation. Such multivalents further lead to the formation of laggards, divide or get eliminated as micronuclei. Non-synchronization of bivalents can be attributed to increased distance between centromere with consequent decrease in repulsion which is regarded as the effective driving force in orientation (Choudhury, 1976). The early separation of some of the bivalents could be ascribed to high percentage of laggards (Amante, 1983). Non-synchronization in the separation of bivalents is caused by change in homology of chromosome partners and many multivalents lead to aneuploid gametes.

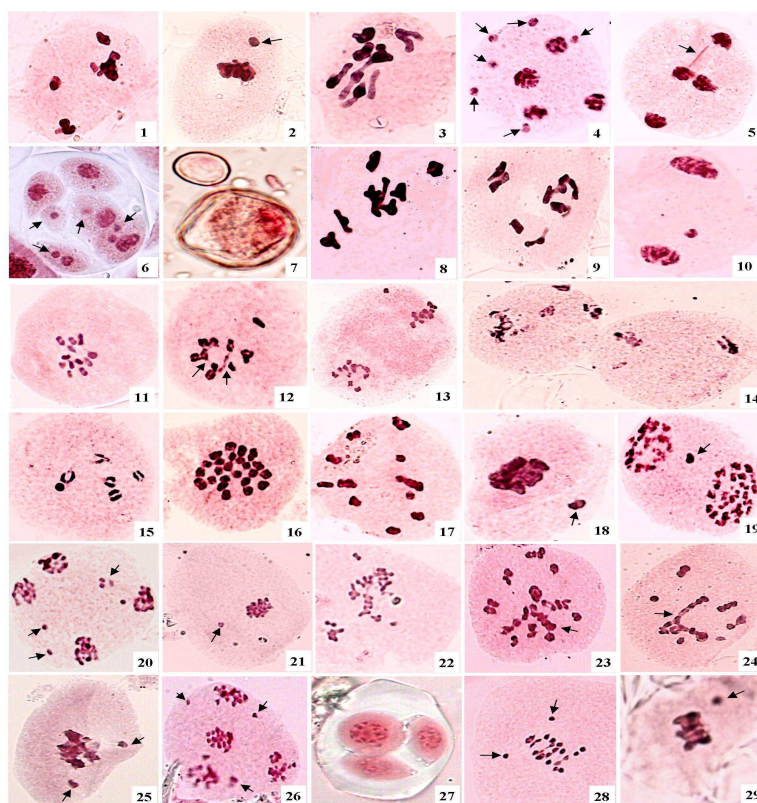
The formation of laggards is attributed to late disjunction of chromosomes, delayed terminalisation and stickiness of chromosome ends or because of failure of chromosome movement. It is mainly due to late alignment of chromosome pairs in metaphase plate. Choudhury (1976) described that late separation of bivalents is quite distinct from bridge formation. However Demeterio *et al.* (1965) explained that bridge formation is mostly due to the delayed disjunction followed by terminalisation of chiasmata (Pagliarini, 2000). Bridge formation may be due to inversion heterozygosity. However the presence of bridges not necessarily indicates the inversion heterozygosity as mentioned by Hseih and Oka (1958). Mehra (1982) explained that these bridges are the result of paracentric inversions.

Sporogenesis is the developmental process which involves production of four haploid spores from a diploid sporocyte by meiosis and cytokinesis. Microsporogenesis is the production of microspores from microsporocytes in heterosporous plants. Any discrepancy during microsporogenesis leads to abnormal microsporogenesis which includes formation of monads, dyads, triads, tetrads, polyads with or without micronuclei. Formation of monads, dyads and triads is due to failure of cytokinesis which is divided into two types: first division restitution (FDR) and second division restitution (SDR). In FDR, usually failure of chromosome segregation at anaphase-I leads to restitution nucleus, the monads. While in



SDR, failure of chromosome segregation at anaphase-II leads to unreduced gametes, the dyads. Failure of cytokinesis in one of the poles during anaphase-II leads to formation of triads. Uneven cytokinesis leads to the formation of polyads. Micronuclei formation is correlated with laggards. Abnormal microsporogenesis with micronuclei formation causes pollen grain sterility. Unreduced pollen grains have significant role from evolutionary point of view.

High levels of meiotic irregularities obviously compromise pollen viability. It has been suggested that infertility in polyploids is not solely due to production of aneuploid gametes formed by improper segregation of chromosomes during anaphase and telophase stages, the genetic factor also bring about pollen sterility as evidenced in different tetraploid plants of rye and *Avena sativa* (Baptista-Giacomelli *et al.*, 2000).



**Figure Legends: Meiotic Observations in Investigated taxa (Scale bar = 10  $\mu$ m)**

Figures 1-7 *Cestrum elegans*, 1  $2n = 16$  at metaphase-I; 2 Chromatin stickiness at metaphase-I; 3 Unoriented bivalent at metaphase-I; 4 Micronuclei at telophase-II; 5 Chromatin bridge at telophase-II; 6 Tetrad with micronuclei; 7 Heterogeneous sized sterile and fertile pollen grains; 8-10 *Cestrum nocturnum*, 8  $2n = 16$  at metaphase-I; 9 Associations of bivalents at metaphase-I; 10 Chromosomal associations at anaphase-I; 11-15 *Datura stramonium*, 11  $2n = 24$  at metaphase-I; 12 Associations of bivalents at metaphase-I; 13 Laggards at telophase-I; 14 Two PMCs involved in cytomixis; 15 PMC at diakinesis with lower chromosome number,  $2n=10$ ; 16-20 *Nicotiana tabacum*, 16  $2n = 48$  at metaphase-I; 17 Metaphase-I showing secondary associations of bivalents; 18 Unoriented bivalent at metaphase-I; 19, 20 Laggards at anaphase-I and anaphase-II; 21-22 *Physalis angulata*, 21 Associations of bivalents at metaphase-I; 22 Unoriented bivalent at metaphase-I; 23-27 *Physalis peruviana*, 23, 24 Secondary associations of bivalents at metaphase-I; 25 Unoriented bivalents at metaphase-I. 26 Laggards at telophase-II; 27 Triad. 28 *Solanum pseudocapsicum*, 28 Early separation of 6 bivalents at metaphase-I; 29 *Solanum verbascifolium*, 29 Chromatin stickiness at metaphase-I.



## CONCLUSIONS

As the only meiosis that decides the fate of chromosomes throughout the sexual life cycles, the variant meiotic errors may possibly result in various genomic variations, including variation in the chromosomal structure, number and ploidy level.

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